

Common Variants of the Oxytocin Receptor Gene Do Not Predict the Positive Mood Benefits of Prosocial Spending

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Who benefits most from helping others? Previous research suggests that common polymorphisms of the oxytocin receptor gene (*OXTR*) predict whether people behave generously and experience increases in positive mood in response to socially focused experiences in daily life. Building on these findings, we conducted an experiment with a large, ethnically homogenous sample ($N = 437$) to examine whether individual differences in three frequently studied single nucleotide polymorphisms of *OXTR* (rs53576, rs2268498, rs2254298) also predict differences in the positive mood benefits of financial generosity. Consistent with past research, participants who were randomly assigned to purchase items for others (vs. themselves) reported greater positive affect. Contrary to predictions, using Bayesian statistics, we found conclusive evidence that the benefits of generosity were not moderated by individual differences in *OXTR* single nucleotide polymorphisms. The current work highlights the importance of publishing null results to build cumulative knowledge linking neurobiological factors to positive emotional experiences.

Keywords: prosocial behavior, positive mood, behavior genetics, individual differences

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Numerous studies have demonstrated the power of prosocial behavior, showing that helping others is associated with enhanced moods, better relationships, and improved physical health (Brown, Nesse, Vinokur, & Smith, 2003; Dunn, Aknin, & Norton, 2008; Klein, 2017; Konrath & Brown, 2013; Van Tongeren, Green, Davis, Hook, & Hulseley, 2016; Whillans, Dunn, Sandstrom, Dickerson, & Madden, 2016; cf. Whillans, Seider, et al., 2016). Although numerous studies have documented a multitude of well-being benefits stemming from prosociality (Aknin, Whillans, Dunn, & Norton, in press; Dunn, Aknin, & Norton, 2014; Konrath, 2014), fewer studies have examined individual differences in the positive mood benefits of helping others. There has been an increased recognition that neurobiological factors can shape emo-

tional experiences as well as the proclivity to help other people (Chen, Barth, Johnson, Gotlib, & Johnson, 2011; Park, Kahnt, Dogan, Strang, Fehr, & Tobler, 2017; Poulin & Holman, 2013; Poulin, Holman, & Buffone, 2012; Rodrigues, Saslow, Garcia, John, & Keltner, 2009; Saphire-Bernstein, Way, Kim, Sherman, & Taylor, 2011; Tost et al., 2010). Bringing together these divergent areas of research, the goal of the current work was to evaluate the role of neurobiological factors in predicting the positive mood benefits of prosocial behavior. Specifically, we sought to examine whether individual genetic differences in the oxytocin system modulate the immediate positive mood benefits of engaging in financial generosity.

The Emotional Benefits of Prosocial Behavior

A large body of correlational and experimental research has demonstrated that spending one's time and money to help others is associated with greater emotional well-being. For example, prior research has shown that volunteering is associated with higher positive affect, increased life satisfaction, and reduced depression (Borgonovi, 2008; Hong & Morrow-Howell, 2010; Musick & Wilson, 2003; Schwartz & Sendor, 1999; cf. Whillans, Seider, et al., 2016). In a review of 26 experimental, correlational and longitudinal studies, volunteering was shown to have favorable effects on various measures of life satisfaction and well-being (Jenkinson et al., 2013). In a well-cited study of nearly 3,000 adults over the age of 25, people who volunteered reported higher levels of life satisfaction and lower depressive symptomology (Musick & Wilson, 2003). Across studies, the association between

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helping others and various indicators of subjective well-being (SWB) held controlling for variables that could otherwise explain these results, including age, socioeconomic status, gender, physical health, and participation in self-focused social activities, such as organized sports teams and cultural groups (Aknin et al., in press, for a review cf. Creaven, Healy, & Howard, 2018; Piliavin & Siegl, 2007).

Experimental research also points to a similar conclusion: helping other people causally promotes well-being. Helping others, such as by engaging in random acts of kindness, can lead people to experience increases in positive mood (Lyubomirsky, Sheldon, & Schkade, 2005; Nelson, Layous, Cole, & Lyubomirsky, 2016). Spending money to help others also leads to improvements in happiness. For example, after spending \$5 or \$20 on other people, individuals experienced greater positive mood than after spending \$5 or \$20 on themselves (Dunn et al., 2008). The positive mood benefits of prosocial spending have also been documented in rich and poor countries, small-scale traditional societies, antisocial populations, and for toddlers under the age of 2 (Aknin et al., 2013; Aknin, Broesch, Hamlin, & Van de Vondervoort, 2015; Aknin, Hamlin, & Dunn, 2012; Hanniball, Aknin, Douglas, & Viljoen, 2018).

Despite the seemingly ubiquitous relationship between prosocial behavior and positive mood, research suggests that there are critical individual differences that predict who benefits most from helping others (Hill & Howell, 2014; Tkach, 2005). Correlational evidence indicates that the positive mood benefits of generous spending are moderated by self-transcendent values (Hill & Howell, 2014). In this research, people who report higher concern for others or entities outside of themselves are more likely to experience the mood benefits of spending money on others. In addition, people who are experiencing life stressors also appear to benefit most from formal volunteering (Schreier, Schonert-Reichl, & Chen, 2013; Van Willigen, 2000; Wheeler, Gorey, & Greenblatt, 1998). Moreover, neurological evidence suggests that the positive mood benefits of financial generosity can be moderated by cultural factors and past family experience (Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010).

Oxytocin and Social-Emotional Functioning

Although research has documented numerous psychological factors that predict the positive mood benefits of helping others, less research has explored neurobiological factors that predict the well-being benefits of helping others (cf. Poulin & Holman, 2013; Bekkers, Konrath, & Smith, 2016). One underexplored factor that may predict the mood benefits of prosocial behavior involves differences in the functioning of the oxytocin system. Although numerous neuropeptides influence cognition and behavior, four decades of research indicate that oxytocin plays a central role in regulating the formation and maintenance of mammalian attachment bonds—implicating oxytocin as a key antecedent of prosocial behavior (Carter, 2014; MacDonald & MacDonald, 2010). Individual differences in the oxytocin receptor gene (*OXTR*)—which encodes the oxytocin receptor protein—are theorized to influence social-emotional functioning by affecting the strength of the oxytocin signal in the brain. Research has linked several common SNPs (single nucleotide polymorphisms) of *OXTR* to individual differences in social-emotional functioning. In individ-

ual studies, *OXTR* has been associated with differences in empathy, prosocial behavior, positive affect, and emotional responsivity to one's children (details on studies provided below; see Kumsta & Heinrichs, 2013, for a review).

Three meta-analyses currently exist that examine links between *OXTR* SNPs and social traits in the general population (Bakermans-Kranenburg & van IJzendoorn, 2014; Gong et al., 2017; Li et al., 2015). In the first meta-analysis (Bakermans-Kranenburg & van IJzendoorn, 2014), no overall association was observed between either the *OXTR* SNP rs53576 (48 samples, $N = 17,559$) or the *OXTR* SNP rs2254298 (34 samples, $N = 13,547$) and phenotypic outcomes in five domains (biology, personality, social behavior, psychopathology, and autism). However, an updated meta-analysis examined whether genetic differences in *OXTR* were predictive of sociality while distinguishing between how individuals respond to people in general (e.g., trait levels of empathy and response to social rewards), and/or how individuals respond to close others, such as offspring and romantic partners (Li et al., 2015). In this meta-analysis, an association was observed between the *OXTR* SNP rs53576 and general sociality (24 samples, $N = 4,955$), but not social or emotional responses in the context of close relationships (15 samples, $N = 5,262$; Li et al., 2015). In another recent study that included both a population-based replication study ($N = 1,830$) and a meta-analysis of 13 independent samples ($N = 6,631$), a robust association was observed between the *OXTR* SNP rs53576 and trait empathy, which is a critical affective antecedent of prosocial behavior (Gong et al., 2017). Overall, these meta-analyses provide some support for the proposition that individual differences in the oxytocin receptor gene can influence social and emotional functioning.

Context-Specific Relationships Between Oxytocin and Emotional Reactions During Socially Focused Experiences

One reason for the mixed findings in existing research may be that oxytocin is linked to phenotypic outcomes in a more context-dependent manner than has typically been accounted for (see Bartz, Zaki, Bolger, & Ochsner, 2011; Shamay-Tsoory & Abu-Akel, 2016). In other words, individual differences in the functioning of the oxytocin system may be most readily observable in the context of a social experience that can trigger a specific emotional reaction. Most relevant to the current investigation, new research has found evidence that individual differences in the functioning of the oxytocin system predict positive emotional responses specifically in the context of social experiences (e.g., Algoe, Kurtz, & Grewen, 2017; Algoe & Way, 2014; Isgett et al., 2017; Isgett, Algoe, Boulton, Way, & Fredrickson, 2016).

In one experimental study, healthy adults were randomly assigned over 6 weeks to complete one of two meditation interventions—loving kindness or mindfulness—designed to increase positive mood (Isgett et al., 2016). These interventions differ in one theoretically important way: Loving kindness meditation involves cultivating warm, tender, compassionate feelings toward others, whereas mindfulness meditation training involves focusing on the present moment (Isgett et al., 2016). Given this difference, the authors predicted that individual differences in *OXTR* would moderate the positive mood benefits of the socially focused intervention (loving kindness meditation), but not of the mindfulness

intervention. Although results were mixed across five SNPs examined, the *OXTR* SNP rs1042778 predicted the extent to which participants' daily experiences of positive mood (e.g., interest, awe, hope) increased over the study in response to the loving kindness intervention.

In another related study, researchers investigated the association between individual differences in the functioning of the oxytocin system and the positive mood benefits of daily social interactions (Isgett et al., 2017). Participants recorded their daily experiences as well as the extent to which these experiences involved other people. Participants with higher levels of circulating oxytocin, who spent more time engaged in experiences that involved other people (such as socializing and helping), reported greater positive mood benefits from engaging in these activities (Isgett et al., 2017). Individual differences in oxytocin did not predict the frequency by which participants engaged in socially focused activities. From this study, the authors concluded that individual differences in the oxytocin system influenced affective processing as opposed to influencing general social approach behavior.

Two additional studies have examined the role of oxytocin (including variation of *CD38*, a gene encoding a glycoprotein that affects oxytocin secretion) in emotional reactions within social contexts involving gratitude. In one study, a polymorphism (rs6449182) that affects *CD38* expression was significantly associated with global relationship satisfaction, perceived partner responsiveness and positive emotions (particularly love) after lab-based interactions, observed behavioral expression of gratitude toward a romantic partner in the lab, and frequency of expressed gratitude in daily life (Algoe & Way, 2014). In another related study, 129 adults received expressions of gratitude from their romantic partners in the lab. Higher circulating oxytocin over the prior 24 hr in the receivers was associated with greater perceptions of the expresser's responsiveness and gratitude, as well as greater experienced love (but not general affective reward; Algoe et al., 2017). Overall, these findings provide evidence that individual differences in the oxytocin system can amplify the salience of social information and, in turn, can influence the positive mood benefits that individuals experience in response to socially focused experiences.

***OXTR* Predicting the Positive Mood Benefits of Prosocial Behavior**

Together with the meta-analyses reported above, these studies suggest that individual differences in the functioning of the oxytocin system predict the mood benefits that individuals derive from thinking about, socializing with, and helping others. Specifically, individual differences in the functioning of the oxytocin system shape the positive mood benefits of socially focused activities, such as loving kindness meditation (Isgett et al., 2016), expressing and receiving gratitude from one's romantic partners (Algoe & Way, 2014; Algoe et al., 2017), and engaging in social activities in daily life (Isgett et al., 2017). Additional research suggests that individual differences in the oxytocin receptor gene can shape the health benefits of volunteering (Poulin & Holman, 2013). These studies are corroborated by a recent review of 33 studies, showing that intranasal oxytocin increases the likelihood that healthy adults will express positive emotions in response to social stimuli (see Leppanen, Ng, Tchanturia, & Treasure, 2017). Building on these

findings, we sought to explore whether individual differences in *OXTR* moderate the positive mood benefits that people experience when engaging in prosocial spending. Our study is, to our knowledge, the first experiment to examine the role of oxytocin in emotional responses to actual (as opposed to imagined) instances of prosocial behavior, as well as the first experiment to examine gene by context interactions regarding financial generosity.

Focus of the Study: SNPs Examined in This Study

As described above, a SNP is a variation affecting one nucleotide (A/G, or T/C) within a sequence of DNA. Thus, for a given SNP, some people may be *homozygous G* (in other words, carriers of two copies of the G allele, or 'GG'), whereas others would be *homozygous A* (in other words, carriers of two copies of the A allele, or 'AA'), or *heterozygous AG*. In this research, we examined three *OXTR* SNPs: rs53576 (A/G), rs2254298 (A/G), and rs2268498 (T/C).

We chose the first two SNPs based on existing evidence from multiple studies that they are associated with variation in social-emotional functioning (Kumsta & Heinrichs, 2013). Indeed, rs53576 and rs2254298 are the most well-studied *OXTR* SNPs; both have been linked to clinical diagnoses of autism spectrum disorder in multiple studies (Ebstein, Knafo, Mankuta, Chew, & San Lai, 2012) and variation in the structure and function of the amygdala and hypothalamus, brain regions involved in responses to threat (Inoue et al., 2010; Tost et al., 2010). The third SNP, rs2268498, has not been as extensively studied as the other two. However, it is the only *OXTR* SNP that has been shown to be functional (Reuter et al., 2017). Specifically, genetic expression analyses in human hippocampal tissue have demonstrated that carriers of the C-allele showed twice the messenger RNA transcription rate as carriers of the T-allele (Reuter et al., 2017). We chose to include rs2268498 in the current study given the unique evidence about its functionality.

Of most relevance to the current research, several studies have documented associations between these three SNPs and human prosociality as well as emotionality. The A allele of rs53576 has been linked to reduced trust (Krueger et al., 2012) and empathy (Rodrigues et al., 2009). In one study, A carriers (individuals with either one or two copies of the A allele, i.e., either AG or AA) exhibited lower behavioral and dispositional empathy as compared to individuals who were homozygous for the G allele (Rodrigues et al., 2009). Given that dispositional empathy can moderate the positive mood benefits of prosocial behavior (Tkach, 2005), these results suggest that individual differences in rs53576 could influence the affective benefits of helping others.

Other indirect evidence for the idea that A carriers for rs53576 may experience fewer positive mood benefits from helping others comes from research suggesting that A carriers show fewer traits and behaviors associated with prosociality. The A allele of rs53576 has been associated with lower levels of optimism, mastery, self-esteem (Saphire-Bernstein et al., 2011) and fewer nonverbal displays of prosociality, such as eye contact and smiling, during social interaction. Carriers of the A allele are also judged as less prosocial by unfamiliar raters (Kogan et al., 2011), and mothers carrying the A allele of rs53576 have been shown to be less responsive to their toddlers during problem-solving tasks than those homozygous for the G allele (Bakermans-Kranenburg & van

Ijzendoorn, 2008). G carriers (individuals with either one or two copies of the G allele, i.e., either AG or GG), on the other hand, report being more likely than AA homozygotes to seek social support when emotionally distressed and when it is culturally normative (Kim et al., 2010). G carriers also benefit more after receiving help from others, showing reduced physiological responses to a stressful task upon receiving social support (Chen et al., 2011). Given that individuals who benefit most from receiving social support also typically benefit most from providing support to others (e.g., Deci, La Guardia, Moller, Scheiner, & Ryan, 2006), G carriers might be more sensitive to the social environment. Overall, previous research suggests that the G allele of rs53576 (compared to the A allele) may be associated with greater affective benefits of helping other people.

For the second SNP, rs2254298, existing evidence suggests that individuals homozygous for the G allele may be less sensitive to the social environment than carriers of the A allele. This reduced social sensitivity in carriers of the G allele of rs2254298 may also be linked to experiencing fewer positive mood benefits of prosocial behavior. Parents in one study who were homozygous for the G allele of rs2254298 had lower levels of oxytocin in their blood, which was, in turn, associated with a decreased tendency to touch their children during a social interaction (Feldman et al., 2012). In another study, infants who were homozygous for the G allele were less likely to be classified as securely attached to their primary caregivers (though the direction of effect was contingent on sample ethnicity; Chen et al., 2011), which may indicate less effective use of social support (Chen, Heinrichs, & Johnson, 2017). For adolescent girls who had experienced childhood adversity (mothers' history of recurrent major depressive disorder), those who were homozygous for the G allele reported the highest levels of symptoms of depression, physical anxiety, and social anxiety (Thompson, Parker, Hallmayer, Waugh, & Gotlib, 2011). Relatedly, in another study, the GG homozygous genotype was over-represented in depressed mothers and their families, correlated with lower salivary oxytocin, and was associated with greater risk of psychopathology in their children (Apter-Levy, Feldman, Varkart, Ebstein, & Feldman, 2013). The observed direction of effects has not always been consistent, however: A meta-analysis on the relationship between rs2254298 and autism spectrum disorder (6 samples; $N = 2900$ families, plus 280 cases/440 controls) linked the A allele (rather than the G allele) to higher risk for autism spectrum disorder.

Finally, the third SNP, rs2268498—which has attracted interest due to unique evidence of its functionality—has also been linked to variation in socioemotional functioning in a small number of recent studies. Carriers of the T allele exhibited more accurate social perception and recognition of facial expressions of emotion than those with the CC genotype (Melchers, Montag, Felten, & Reuter, 2015; Melchers, Montag, Markett, & Reuter, 2013). In another study, carriers of the T allele also showed better learning performance of implicit social information while watching social interactions than those with the CC genotype; furthermore, learning performance was positively associated with self-reported empathy and negatively with self-reported autistic traits (Melchers et al., 2017).

Taken together, these findings suggest that variations in *OXTR* may play a critical role in shaping not only who is most likely to engage in prosocial behavior, but also who is most likely to

experience emotional benefits from enacting prosocial behavior in everyday life.

Current Hypotheses

The research reviewed thus far indicates that helping others can have positive mood benefits for the actor. Although this relationship appears to be robust, research suggests that the relationship between helping and happiness can vary as a function of critical individual differences, such as personality and past experiences. Research suggests that individual genetic differences can shape the positive mood benefits of socially focused behaviors (Isgett et al., 2016, 2017). More specifically, research examining the relationship between *OXTR* and social and emotional responsiveness points to the possibility that the relationship between helping and well-being might be influenced, in part, by individual differences in three common variants of *OXTR*: rs53576, rs2254298, and rs2268498. Yet, no research has directly examined whether individual genetic differences predict the positive mood benefits of helping others.

By exploring this question, our research contributes to the literature in several ways, as follows. Prior theorizing and research demonstrates that positive emotions predict prosocial behavior (Fredrickson, 2001; Isen, 1970; Isen & Levin, 1972). Moreover, functional accounts of emotion suggest that positive emotions reinforce prosocial behavior (Aknin, Van de Vondervoort, & Hamlin, 2018). Thus, understanding who stands to gain the greatest emotional benefits from prosocial behavior may help to provide meaningful insight into who is most likely to engage in prosocial action again in the future and, potentially, who stands to benefit most from interventions to encourage prosociality. Understanding whether individual differences in the oxytocin system moderate the benefits of helping others could facilitate a better understanding of the specific contexts where individual genetic differences shape positive emotions. Given the importance of understanding whether and how genetic differences impact the positive consequences of various interpersonal activities, we conducted an experiment to examine whether individual differences in the positive mood benefits of prosociality may be influenced by natural variation in the oxytocin system, as indexed by three common SNPs of *OXTR*.

Based on the largely consistent directional findings reported in prior studies about rs53576 showing that individuals homozygous for the G allele of rs53576 express greater social sensitivity and emotional responsiveness than individuals homozygous for the A allele (for recent meta-analyses, see Gong et al., 2017; Li et al., 2015), we predicted that individuals homozygous for the G allele of rs53576 would experience greater emotional benefits upon providing help to others than carriers of the A allele (AA and AG).¹ Although rs2254298 and rs2268498 have both been linked to social-emotional functioning in humans, it is less clear from prior research what direction of association should be expected between these variants and emotional responses to prosocial giv-

¹ In the existing literature, heterozygotes for rs53576 (AG) are sometimes combined with the AA group ("dominant-allele model"), and sometimes combined with the GG group ("recessive-allele model"). In this study, we take the more common dominant-allele model approach of grouping AA and AG into an "A carrier" group (see also Li et al., 2015).

ing. Consequently, for rs2254298 and rs2268498, we made more conservative nondirectional hypotheses; namely, that variation of these two SNPs would be associated with experiencing emotional benefits from prosocial giving. Because it is unclear whether all three SNPs should contribute additively to positive mood responses to prosocial behavior, we tested associations between our outcome measure and each SNP separately.

Focus of the Study: Prosocial Spending

Prosocial behavior is defined as any action taken with the intention to help other people, as understood and agreed upon by one's self or individuals in one's social group (Penner, Dovidio, Piliavin, & Schroeder, 2005). Although the category of prosocial behavior is broad and diverse, several taxonomy models have been proposed in the literature to organize the diverse forms prosocial behavior can take. For example, synthesizing forms of prosocial behavior from past research, Pearce and Amato (1980) proposed a three-factor model containing the following dimensions (a) spontaneous/informal versus planned/informal, (b) serious versus not serious, and (c) doing/direct versus giving/indirect. More recently, McGuire (1994) offered a four-factor model derived from lay evaluations including casual, substantial, emotional, and emergency helping.

In the current research, we examine the positive mood benefits of *prosocial spending*, which is defined as using money to benefit other people. Consistent with previous definitions (Aknin et al., 2013; Dunn et al., 2014), prosocial spending involves using financial resources to assist other people in various ways, such as by treating family or friends to a meal, donating money to charity, or—as examined in the current article—spending money to purchase a gift for an individual in need. Prosocial spending may be defined in different ways using the taxonomies noted above. However, the form examined here—purchasing a gift for someone in need—is most appropriately considered a casual and spontaneous/informal act of giving/indirect assistance offered in a nonserious manner.

Materials and Method

Overview

To test these hypotheses, we conducted a well powered experiment that was designed to replicate the causal impact of financial generosity on positive mood. To this end, we used an identical protocol from previously published research (Aknin, Barrington-Leigh, et al., 2013) in which participants earned a small sum of money that they were randomly assigned to spend on treats for either themselves (*personal spending*) or another person (*prosocial spending*). Afterward, participants reported their positive affect. In line with past research, we predicted that participants randomly assigned to spend on others would report higher levels of positive affect than those randomly assigned to spend on themselves. Critically, we also examined individual differences in three common variants of the OXTR gene (rs53576, rs2254298, rs2268498) to investigate whether these SNPs moderated the positive mood benefits of financial generosity.

In the goody bag paradigm, which we describe in detail below, participants were randomly assigned to spend a windfall of money

on treats for a sick child at a local children's hospital or on treats for themselves (Aknin et al., 2013). When a purchase was made for a sick child, the recipient was unknown to the giver and the gift was provided through an intermediary, thereby precluding the possibility that givers receive expressions of gratitude or reciprocity. In addition, research assistants and other participants were unaware when a participant committed a prosocial act, reducing the possibility of social praise. As such, this well-validated paradigm minimizes alternative explanations for the positive mood benefits of helping others.

Importantly, the target used in the goody bag paradigm is a vulnerable person. Vulnerable targets elicit tenderness and empathy, even when these targets are not experiencing an urgent need (Lishner, Batson, & Huss, 2011). Presenting participants with a vulnerable target is likely to mobilize the care taking system for which the oxytocin system has evolved (Pedersen, Ascher, Monroe, & Prange, 1982). Indeed, recent review papers and empirical evidence suggest that the effects of natural variation in the oxytocin system extend well beyond mother and child relationships, supporting the development and maintenance of social relationships between strangers, close friends, and romantic partners (Anacker & Beery, 2013; Decety, Bartal, Uzevovsky, & Knaf-Noam, 2016). Empirical evidence with rodent and human samples supports this assertion. In one study, experimentally increasing circulating oxytocin levels shifted rodents' social preferences—such that rodents with higher circulating oxytocin no longer avoided a previously threatening male rat (Lukas et al., 2011). In another study (Lukas et al., 2011), blocking circulating oxytocin lowered rodents' preferences for interacting with novel social stimuli (a male rat they had never seen before) but did not reduce rodents' preferences for interacting with novel asocial stimuli (a toy that they had never seen before). These studies provide evidence that the oxytocin system shifts social behavior even when social interactions do not have implications for pair-bonding, parenting, or reproduction (i.e., male-male interactions; Lukas et al., 2011; Menon et al., 2018).

Related results have also been documented in the context of human prosociality. In one experiment, participants who received an intranasal administration of oxytocin were more generous in a standard dictator regardless of whether the target of their generosity belonged to an in-group or to an out-group (Israel, Weisel, Ebstein, & Bornstein, 2012, see also: Terris, Beavin, Barraza, Schloss, & Zak, 2018). These findings suggest that oxytocin can influence social and prosocial responses even when these responses do not directly involve interactions with close kin, close others, or people with whom one intends to form a relationship. Indeed, the meta-analysis we cited above (Li et al., 2015) suggests that variants of *OXTR* were significantly predictive of general social inclinations, as opposed to social and emotional responses in the context of close relationships. Together, these data suggest that the vulnerable target used in the goody bag paradigm provides a meaningful target for examining the question of whether variants of *OXTR* predict the positive mood benefits of financial generosity.

Statistical Power

We took several steps to maximize statistical power by maximizing internal validity and reducing measurement error. We implemented a well-validated paradigm from past research (Aknin,

Barrington-Leigh, et al., 2013). We also used common and well-validated measures of SWB (Aknin et al., 2013; Diener & Lucas, 1999; Dunn et al., 2008; Whillans, Dunn, et al., 2016). Furthermore, we recruited a homogenous sample of participants of Central European (Caucasian) descent living in Canada to avoid potential spurious correlations that can arise in genetic association studies due to population stratification and potential differences across ethnicities or cultures in our dependent measure (see also Cardon & Palmer, 2003; Hovey et al., 2018; Woods, Bedard, McQuaid, Matheson, & Anisman, 2018). Population stratification occurs when allele frequencies for a specific SNP differ across subgroups of a population (e.g., ethnicities), as has been extensively documented for both rs53576 and rs2254298 (see Butovskaya et al., 2016, for frequency tables).

We also recruited a sample that was large enough to detect a small influence of individual genetic differences on the positive mood benefits of financial generosity. Specifically, our final sample included $N = 437$ participants ($N > 200$ participants per condition). This sample size provided us with 90% power to detect main effects and interactions with a small effect of $r = .15$ or larger between condition assignment and common *OXTR* SNPs on postspending happiness (G*Power, 2013). Given that recent meta-analyses suggest that the effects of the common *OXTR* SNP rs53576 on social behavior represents a small effect (Li et al., 2015), we believe that this sample size provides us with adequate statistical power to examine our key question of interest.

Post hoc power analyses provided us with further evidence that we recruited an adequate sample size. Upon study completion, we completed post hoc power analyses considering the uneven allele distributions that we observed (G*Power, 2013). In these analyses, for rs2268948, we achieved 88% power to detect a small effect of each genetic variant on positive mood in the prosocial spending condition. For rs53576, we achieved 92% power to detect a small effect of each genetic variant on positive mood, and for rs2254298 we achieved 80% power to detect a small effect of each genetic variant on prosocial mood in the prosocial spending condition.

Preregistration, Replicability, and Transparency

In this article, we report all exclusions and every measure given, and we have posted our a priori hypotheses, materials, data, and code through the Open Science Framework (OSF: <https://osf.io/kvrhs>). It is worth noting that we did not formally preregister our study using an OSF template because our lab had not yet implemented a systematic method for preregistering studies through the OSF at the time this study was conducted (2013–2014). However, we have provided a date-stamped grant application that contains our a priori predictions and protocols for interested readers.²

Analyses Overview

Mood benefits. We measured the broad construct of SWB using multiple scales (Kashdan, Biswas-Diener, & King, 2008). However, consistent with past work, we focused our analyses on positive affect (Aknin et al., 2013). For transparency, we include the results on all measures in Table 1. Data for the entire sample is available through the OSF.

Individual genetic differences. We analyzed rs53576, rs2254298, and rs2268948. For rs2268948, we retained three sep-

arate genotype groups (TT, TC, CC) for analysis. For rs53576 and rs2254298, we used a dominant-allele model (i.e., we collapsed AG and AA into a single category of “A allele carriers”). Given the low frequency of the A allele in Caucasian populations for both rs53576 and rs2254298, the AA group was too small to be analyzed separately; use of the dominant-allele model is also the predominant analysis strategy for rs53576 (see Li et al., 2015, for a meta-analysis using this identical strategy).

Participants and Procedure

We recruited a total of 443 Caucasian participants from the University of British Columbia and Simon Fraser University, two public institutions in or near Vancouver, Canada. Participants at both institutions completed the experiment in exchange for course credit. Unless otherwise noted, all procedures described below follow those reported in Study 3 by Aknin et al. (2013). Six participants opted out of making a purchase in the prosocial spending condition and were excluded from analyses because they did not complete a prosocial act; results do not change if these individuals are included. This decision left us with a final sample of 437 participants (75.5% female; see Table 2 for demographic characteristics).

Participants were run through the experiment in small group sessions. Because participants had to provide a saliva sample, each participant was seated at his or her own individual table or behind a 2.5-foot cardboard partition to provide a personal and confidential space for study completion.³ This methodological detail differed from Aknin et al. (2013). The researcher provided each participant with a questionnaire packet that contained the baseline well-being measures and condition assignment information.

Baseline positive mood. In the questionnaire packet, participants reported their general happiness on a single-item measure (“How happy are you right now?”) on a 5-point scale ranging from 1 (*not at all*) to 5 (*extremely*; Abdel-Khalek, 2006) and on a single-item version of the Subjective Happiness Scale (Lyubomir-

² Hypotheses in the grant refer to rs53576 only, and Study 2 in the grant application was not run. Other than these modifications, the goody bag protocol that is outlined in the grant application is identical to the protocol that we used in this study.

³ We also took several precautions to ensure that our study results were not influenced by the fact that we collected data during group testing sessions. First, participants in all group testing sessions were seated behind 2.5-foot cardboard dividers. This ensured that participants had privacy during the study and could not easily see other participants’ responses. Second, we randomly assigned participants within each group testing session to both spending conditions. Thus, if group size were to impact mood, it would have likely impacted the mood of all participants (in both conditions) within a session. These precautions suggest that it is unlikely that the mood benefits observed were driven by group size. Indeed, several analyses using all available data on group size collected ($n = 166$) support this interpretation. First, group size was not related to participants’ baseline levels of happiness ($r = -0.01$, $p = 0.879$). Second group size did not interact with condition to predict Time 2 positive affect ($\beta = 0.07$, $p = 0.511$). Finally, there were no three-way interactions between Condition \times Group Size \times Genotype (rs53576; $\beta = 0.09$, $p = 0.813$, rs2268948; $\beta = -0.01$, $p = 0.908$; rs2254298; $\beta = 0.03$, $p = 0.877$) to predict T2 positive affect. Given that we did not have this variable available for all participants who completed the study and given that group size did not predict any of our key outcomes of interest, we did not include group size as a covariate in our main analyses reported in text (to preserve the statistical power of our core analyses).

Table 1
Condition Predicting Emotional Benefits

Analysis	Prosocial spending (<i>n</i> = 218)	Personal spending (<i>n</i> = 219)	Statistics
T2 positive affect, no control variables	2.91 (.73)	2.77 (.67)	$F(1, 435) = 4.453, p = .035$
T2 positive affect, controlling for T1 mood	2.91 (.73)	2.77 (.67)	$F(1, 433) = 5.675, p = .018$
T2 negative affect, no control variables	1.20 (.27)	1.29 (.40)	$F(1, 435) = 7.542, p = .006$
T2 negative affect, controlling for T1 mood	1.20 (.27)	1.29 (.40)	$F(1, 433) = 8.199, p = .004$
T2 satisfaction with life, no control variables	5.16 (1.16)	5.11 (1.14)	$F(1, 435) = .215, p = .643$
T2 satisfaction with life, controlling for T1 mood	5.16 (1.16)	5.11 (1.14)	$F(1, 433) = .217, p = .641$

sky & Lepper, 1999). As expected, the two baseline measures of SWB were significantly correlated, $r(435) = 0.49, p < .001$. These scales were standardized and combined to create a broad measure of baseline positive mood. At baseline, participants also reported how “alert,” “tired,” “sad,” and “hungry,” they were currently feeling on a 5-point scale ranging from 1 (*not at all*) to 5 (*extremely*). These items were included as filler questions to mask our interest in mood. Given that the purpose of these items was to serve as filler questions, we do not discuss them further.

Purchasing task. The next page of the questionnaire packet told participants that they had earned a small monetary sum of \$2.50, presented in the form of a paper voucher, as additional compensation for their participation. Participants were asked to sign a page of their questionnaire package to acknowledge receipt and take ownership of the funds. Then, on the next page of the questionnaire, participants were informed that they could use their additional funds to purchase a “goody bag” filled with candy and/or juice at a discounted price (i.e., purchase \$3.00 worth of items for \$2.50). Specifically, participants could choose between a

goody bag that contained two juice boxes, two small chocolate bars, or one juice box and one chocolate bar.

Participants randomly assigned to the personal spending condition selected the items for themselves. Participants randomly assigned to the prosocial spending condition selected the items that would be donated to a sick child at a local children’s hospital. Because past research has demonstrated that a sense of volition is essential for experiencing the hedonic rewards of prosocial behavior (Weinstein & Ryan, 2010), participants in both conditions also had the opportunity to opt-out of purchasing a goody bag and take the cash value (\$2.50) for themselves. This option ensured that individuals in the prosocial spending condition felt as though they had chosen to give a charitable gift. See the [supplemental appendix](#) in the online supplemental material for the full study protocol.

In both spending conditions, participants indicated their spending decision on a purchase card and took this card, along with the \$2.50 voucher, to a researcher in an adjacent room. In both conditions, if the participant had purchased a goody bag, the researcher packaged their items immediately to indicate to the participant that their goody bag was real. In both conditions, the goody bag was marked with the participants’ unique identifier and was set aside until the conclusion of the experiment. Participants were then given a preprepared note that thanked them for their purchase. If a participant took the cash for herself, she was asked to provide her e-mail address to schedule a time for pick-up. Critically, of the all information that indicated participants’ condition assignment was kept from the researchers who were interacting with participants to avoid differential treatment. We also ensured that the study materials were organized well in advance by a researcher who did not conduct the experimental sessions. All study materials seen by researchers (e.g., questionnaires, purchase cards, money vouchers) were identical for both conditions. As such, the researcher only learned of the participants’ condition assignment at the very end of the experiment, after participants had completed our all measures, to give participants assigned to the personal spending condition their goody bag. The goody bags purchased in the prosocial spending condition were donated to a local children’s charity.

Postspending mood. After completing the spending task, participants were given a second questionnaire package to report their current positive affect on the Positive and Negative Affect Schedule (PANAS; positive affect, $\alpha = .82$, and negative affect, $\alpha = .79$; Watson, Clark, & Tellegen, 1988), which included the word *happy* on a 5-point scale ranging from 1 (*very slightly or not at all*) to 5 (*extremely*). Participants also reported their overall life satisfaction on the Satisfaction with Life Scale (SWLS; $\alpha = .87$;

Table 2
Demographic Characteristics of Sample

Variable	<i>M</i> or %	<i>n</i>
Female	75.5%	437
Age	20.71 (4.06)	437
Financial situation during the last year		
I could save money	40.3%	422
I just got by	16.5%	
I spent some savings	33.0%	
I spent savings and borrowed money	6.9%	
rs53576		415
GG	42.9%	
AG	45.5%	
AA	11.6%	
rs2254298		423
GG	80.9%	
AG	17.7%	
AA	1.4%	
rs2268498		421
TT	27.1%	
TC	48.2%	
CC	24.7%	

Note. The sample size does not reach 437 in all analyses given that some of the saliva samples were unanalyzable (either we had no ethnicity data or the participant did not produce enough saliva for the genotype data to be extracted) and because some participants chose not to answer the questions (and we could not make the questions mandatory for participants).

Diener, Emmons, Larsen, & Griffin, 1985) on a 7-point scale ranging from 1 (*strongly disagree*) to 7 (*strongly agree*). As described above, we focused our analyses on positive affect (see also: Akinin et al., 2013). Finally, participants completed demographic measures, including a 1-item measure of financial stability, ethnicity, gender, and age. See the [supplemental appendix](#) in the online supplemental material for a full list of measures.

Genotyping. Saliva samples were collected using the Oragene Kit (DNA Genotek, Ottawa, Ontario, Canada) that allowed for the collection, preservation, transportation and purification of DNA. Participants were instructed not to brush their teeth, eat, or drink beverages containing alcohol or caffeine 30 min before taking the sample. Samples were genotyped using TaqMan® assays (rs53576 [Celera_ID: C_3290335_10], rs2254298 [Celera_ID: C_15981334_10], rs2268498 [Celera_ID: C_15874460_10]; Applied Biosystems). TaqMan® PCR reactions were done with Universal Master Mix Amperase® UNG, 0.50uL Taqman probe mix and 4.5uL of DNA 5 ng/μl in water for a 10uL total volume. The PCR conditions for the TaqMan® SNP Genotype Assays were one AmpErase® step at 50.0°C for 2 min, one enzyme activation step at 95.0°C for 10 min, and 40 alternating cycles of denaturation at 92.0 °C for 15 s and reannealing and extension at 60.0°C for 1 min. All PCR reactions were performed on ABI 7500 fast Real-time PCR Instrument (Applied Biosystems, Foster City, CA). The fluorescence intensity of the final PCR product was measured using an LjL Analyst AD fluorescence microplate reader (LjL Biosystems, Sunnyvale, CA, www.moleculardevices.com) using LjL CriterionHost Software.

To test for associations among the three SNPs, we calculated r^2 , a measure of linkage disequilibrium, using publicly available data on all Central European populations from 1,000 genomes (Phase 3, October 2014). Linkage disequilibrium was negligible between rs53576 and rs2254298 ($r^2 = .03$) as well as between rs53576 and rs2268498 ($r^2 = .02$). Linkage disequilibrium between rs53576 and rs2268498 was low to moderate ($r^2 = .22$). Given these low associations, we retained all three SNPs as independent predictors in our analyses.

Results

Emotional Benefits of Prosocial Spending

We first assessed whether participants randomly assigned to purchase a goody bag for charity reported greater postspending positive affect than participants randomly assigned to purchase a goody bag for themselves. To address this question, we submitted postspending positive affect reports to a one-way between subjects analysis of variance (ANOVA).

Replicating previous research and consistent with our prespecified hypotheses, participants randomly assigned to the prosocial spending condition reported significantly higher positive affect ($M = 2.91$, $SD = 0.73$) than participants in the self-spending condition ($M = 2.77$, $SD = 0.67$), $F(1, 435) = 4.45$, $p = .035$, $d = 0.20$. The main effect of condition remained statistically significant when baseline happiness was added as a covariate, $F(1, 433) = 5.68$, $p = .018$.⁴

Individual Genetic Differences

Allele frequencies for each SNP in our sample are reported in Table 2 and are comparable to those reported previously in European samples (Butovskaya et al., 2016; Montag, Fiebach, Kirsch, & Reuter, 2011). All three SNPs were in Hardy-Weinberg equilibrium (rs53576: $p = .66$; rs2268498, $p = .51$; rs2254298: $p = .90$), which suggests that the allele frequencies are stable in this population.

We examined whether the three key OXTR SNPs of interest—rs53576, rs2254298, rs2268498—moderated the positive mood benefits of prosocial spending. To examine this question, we submitted postspending positive affect reports to three separate two-way ANOVAs whereby condition assignment and oxytocin SNPs were entered as between-subjects factors. In contrast to our predictions, we found no interaction between condition and any of the SNPs (all F s < 0.50 , all p s > 0.60 ; Tables 3–5). These conclusions did not change when baseline happiness was added as a covariate (Tables 6–8). These results suggest that the mood benefits of prosocial spending were not impacted by individual genetic differences in the three key OXTR SNPs assessed in this study—rs53576, rs2254298, and rs2268498.⁵

Bayesian Analyses

Because null results cannot confirm the absence of an effect, we conducted Bayesian analyses to quantify the amount of evidence provided by the null individual genetic difference results above. For each analysis, we computed Bayes factors to determine whether the observed data supported the alternative models or the null model. Following the work of Rouder, Morey, Speckman, and Province (2012), a Cauchy prior distribution was used to represent the likelihood of potential effect sizes in the alternative models. Then, for each alternative model, the analysis produced a Bayes factor, BF_{10} , which was the ratio of the likelihoods of obtaining the observed data under the alternative versus the null hypothesis. For example, if $BF_{10} = 3$, it is three times as likely to obtain the observed data under the alternative hypothesis than the null hypothesis, pre-

⁴ On an exploratory basis, we also examined whether condition assignment predicted negative mood. As evidenced in Table 3, participants randomly assigned to the prosocial spending condition reported significantly lower negative mood ($M = 1.20$, $SD = 0.27$) as compared to participants randomly assigned to the self-spending condition ($M = 1.29$, $SD = 0.40$), $F(1, 435) = 7.54$, $p = 0.006$. The main effect of condition remained statistically significant when baseline happiness was added as a covariate, $F(1, 433) = 8.20$, $p = 0.004$. As indicated in Table 3, and consistent with previous research (Akinin et al., 2013), there was no effect of condition assignment on overall life satisfaction in this study. Because we were primarily interested in the influence of prosocial spending on positive affect, we do not discuss these additional well-being measures further. Our full data is available through the OSF.

⁵ On an exploratory basis, we examined whether the positive mood benefits of prosocial spending were strongest for respondents who reported the highest levels of financial distress in the past year. This analysis is consistent with past research showing that providing help to others can improve well-being by protecting individuals from the negative impact of stress (Poulin et al., 2013; Raposa, Laws, & Ansell, 2016). Inconsistent with this hypothesis, there was no interaction between condition and distress to predict positive mood ($p = 0.634$). Because this was not our key analysis of interest, we did not follow up on this result further.

Table 3
Descriptive Statistics for T2 Positive Affect, by Condition and rs53576

Condition	rs53576	<i>M</i>	<i>SD</i>	<i>n</i>	Statistics
Personal spending	GG	2.80	.74	89	
	AG/AA	2.78	.58	114	
	Total	2.79	.65	203	
Prosocial spending	GG	2.91	.64	85	
	AG/AA	2.97	.79	115	
	Total	2.94	.72	200	
Total	GG	2.85	.69	174	
	AG/AA	2.87	.69	229	
	Total	2.87	.69	403	
Condition predicting T2 positive affect, interaction with rs53576					
Condition					$F(1, 399) = 4.754, p = .030$
rs53576 (GG vs. AG/AA)					$F(1, 399) = .066, p = .797$
Condition \times rs53576					$F(1, 399) = .244, p = .622$
Condition predicting T2 positive affect, interaction with rs53576 controlling for T1 subjective well-being					
T1 SWB composite					$F(1, 398) = 119.585, p < .001$
Condition					$F(1, 398) = 5.947, p = .015$
rs53576 (GG vs. AG/AA)					$F(1, 398) = .062, p = .804$
Condition \times rs53576					$F(1, 398) = .431, p = .512$

senting notable evidence for the alternative hypothesis. It follows that if $BF_{10} = 1$, there is equal evidence for the alternative hypothesis and the null hypothesis. Finally, if $BF_{10} = .33$, it is less than one third as likely to obtain the observed data under the alternative hypothesis than the null hypothesis, presenting notable evidence for the null hypothesis.

Bayes factors for the ANOVA models were computed using the Bayesian ANOVA module under JASP, which uses the R package BayesFactor (Morey & Rouder, 2015). For each of the three key SNPs, three models predicting postspending positive affect were defined as (a) a null model containing only the effect of the prosocial spending conditions; (b) an alternative model containing the effect of genetic differences in addition to prosocial spending conditions; and (c) a second alternative model containing the effect of genetic differences, prosocial

spending conditions, and the interaction between genetic differences and prosocial spending.

Although the JASP software set the scale parameter of the fixed effect Cauchy prior to .5 by default, such a large alternative prior would unreasonably favor the null hypothesis if the effect size that we were to expect was small. Because the effect of genetic differences was likely to be small based on meta-analyses of previously published research (Li et al., 2015), we decided to set a more conservative prior with a scale parameter of .15.

For the three SNPs, rs53576, rs2254298, and rs2268498, we obtained Bayes factors for the main effect models of genetics, $BF_{10} = .332, .286, \text{ and } .379$, and Bayes factors for the interaction models of genetics, $BF_{10} = .151, .096, \text{ and } .175$ (Tables 6–8). These small Bayes factors presented substantial evidence that

Table 4
Descriptive Statistics for T2 Positive Affect, by Condition and rs2254298

Condition	rs2254298	<i>M</i>	<i>SD</i>	<i>n</i>	Statistics
Personal spending	GG	2.79	.62	165	
	AG/AA	2.74	.80	42	
	Total	2.78	.66	207	
Prosocial spending	GG	2.93	.75	167	
	AG/AA	2.96	.62	37	
	Total	2.93	.73	204	
Total	GG	2.86	.69	332	
	AG/AA	2.85	.73	79	
	Total	2.85	.70	411	
Condition predicting T2 positive affect, interaction with rs2254298					
Condition					$F(1, 407) = 4.232, p = .040$
rs2254298 (GG vs. AG/AA)					$F(1, 407) = .001, p = .977$
Condition \times rs2254298					$F(1, 407) = .206, p = .650$
Condition predicting T2 positive affect, interaction with rs2254298 controlling for T1 subjective well-being					
T1 SWB composite					$F(1, 406) = 122.351, p < .001$
Condition					$F(1, 406) = 7.836, p = .005$
rs2254298 (GG vs. AG/AA)					$F(1, 406) = .072, p = .788$
Condition \times rs2254298					$F(1, 406) = 1.656, p = .199$

Table 5
Descriptive Statistics for T2 Positive Affect, by Condition and rs2268498

Condition	rs2268498	<i>M</i>	<i>SD</i>	<i>n</i>	Statistics
Personal spending	TT	2.85	.73	59	
	CT	2.78	.61	94	
	CC	2.67	.71	60	
	Total	2.77	.67	213	
Prosocial spending	TT	2.92	.55	55	
	CT	2.91	.78	109	
	CC	2.90	.82	44	
	Total	2.91	.73	208	
Total	TT	2.88	.65	114	
	CT	2.85	.71	203	
	CC	2.77	.76	104	
	Total	2.84	.71	421	
Condition predicting T2 positive affect, interaction with rs2268498					
Condition					$F(1, 414) = 3.721, p = .054$
rs2268498 (TT vs. TC vs. CC)					$F(2, 414) = .545, p = .581$
Condition \times rs2268498					$F(2, 414) = .364, p = .695$
Condition predicting T2 positive affect, interaction with rs2268498 controlling for T1 subjective well-being					
T1 SWB composite					$F(1, 414) = 118.908, p < .001$
Condition					$F(1, 414) = 5.505, p = .019$
rs2268498 (TT vs. TC vs. CC)					$F(2, 414) = 1.089, p = .337$
Condition \times rs2268498					$F(2, 414) = .824, p = .439$

genetic differences had no effect on the emotional benefits of prosocial spending above and beyond participants' assigned spending conditions.

Discussion

In a sufficiently powered study with more than 400 subjects, individuals randomly assigned to spend money on others reported significantly greater positive affect after making a material purchase for someone else rather than for themselves. Individual genetic differences in the oxytocin system did not influence the positive affective benefits of financial generosity.

The positive affect results in this experiment replicate a growing body of research demonstrating that financial generosity promotes momentary happiness. These results also cast doubt on the possibility that the positive mood benefits of financial generosity vary as a function of individual differences affecting the oxytocin system. We found no interaction between condition and three well-documented individual differences related to the functioning of the oxytocin system (indexed by variability of rs53576, rs2254298, and rs2268498). Using Bayesian statistics, the null model indicating no effect was more likely to have produced our data.

The present research expands existing work in this area by examining whether genetic factors influence people's positive emotional responses. Past research has found evidence that

individual differences in *OXTR* predict prosocial responding (Kogan et al., 2011) and that these differences can amplify the stress-buffering benefits of formal volunteering (Poulin & Holman, 2013). Yet, it appears that individual differences in three common *OXTR* SNPs do not predict whether individuals derive positive mood benefits from acts of financial generosity. Of course, it may be the case that the effects of individual genetic differences on our outcome measure are simply too small to have been detected in this study. If true, this would cast doubt on the possibility that these individual genetic differences play an important role in promoting the mood benefits of helping, given that our study was adequately powered to detect small effects.

Relatedly, these results suggest that the previously reported effects of variability in *OXTR* on social-emotional functioning may not be as robust or generalizable as previously assumed. Indeed, recent *OXTR* meta-analyses have yielded mixed findings (Bakermans-Kranenburg & van IJzendoorn, 2014; LoParo & Waldman, 2015; McCullough, Churchland, & Mendez, 2013; Ritveld et al., 2013). Similarly, recent meta-analyses have critiqued the robustness of intranasal oxytocin administration effects (Nave, Camerer, & McCullough, 2015). As in many other areas of research, methodological concerns, publication biases, and "file-drawer" issues may have contributed to the mixed findings in this field. As such, many scholars have called upon future research to

Table 6
Bayesian Analysis of Variance Model Comparisons for the Effects of rs53576

Models	P(M)	P(M data)	BF _M	BF ₁₀	error%
Condition	.333	.674	4.137	1.000	
Condition + rs53576	.333	.224	.557	.332	.797
Condition + rs53576 + Condition \times rs53576	.333	.102	.227	.151	1.074

Table 7
Bayesian Analysis of Variance Model Comparisons for the Effects of rs2254298

Models	P(M)	P(M data)	BF _M	BF ₁₀	error%
Condition	.333	.644	3.612	1.000	
Condition + rs2254298	.333	.244	.645	.379	.763
Condition + rs2254298 + Condition × rs2254298	.333	.113	.254	.175	3.387

replicate these results with larger samples and improved methodologies (Lane, Luminet, Nave, & Mikolajczak, 2016; Leng & Ludwig, 2016; Walum, Waldman, & Young, 2016), which is a key contribution of the present research.

It is worth noting that many of the specific critiques of recent research on *OXTR* are based on a fundamental skepticism that SNPs can explain meaningful variation in the often highly complex behaviors that researchers have targeted in recent years as dependent variables. We share this skepticism. We chose to investigate the positive mood benefits of prosocial behavior as our dependent measure because we believe that these positive mood benefits are a plausible extension of the basic functions that oxytocin might have evolved to regulate across mammalian species (Carter, 2014; MacDonald & MacDonald, 2010). That said, the null results we obtained on emotional outcomes fit with the most recent literature suggesting that more powerful designs are needed to understand whether, when, and how individual differences in *OXTR* predict social and emotional functioning.

Indeed, it is important to keep in mind the scope of the current research. As discussed in the introduction, we took several steps to increase the internal validity of this research by using a well-validated paradigm and recruiting a homogenous sample of Caucasian participants. By conducting this study in a lab context using a validated experimental protocol, our research provides a tightly controlled test of our core hypotheses. Despite the artificiality of the lab context, the goody bag paradigm provided our participants with the chance to purchase a small gift for another person—a form of prosocial spending that individuals commonly encounter in daily life. Of course, the lab context is unlikely to be as emotionally provocative as helping someone in the context of daily life. As a result, the giving situation could have felt artificial to participants, potentially dampening both the positive mood benefits of prosocial spending as well as the responsivity of the oxytocin system. Given these limitations, our study likely provides a conservative test of our hypothesis. Building on our results and the work of Isgett et al., 2016, future work should examine the role of the oxytocin system for influencing the mood benefits of prosocial spending in daily life.

Relatedly, we used a paradigm that enabled participants to engage in an act of generosity that could not result in social praise or feelings of social belonging (Aknin et al., 2013). For instance, we did not include measures that enabled participants to help friends, family members, or romantic partners. This research raises the possibility that interactions between *OXTR* SNPs and the positive mood benefits of prosociality may be more readily detectable to the extent that the acts of helping provide actors with an opportunity to strengthen preexisting social bonds or forge new bonds. This possibility would be consistent with oxytocin's observed role in the parent-infant attachment bonds and monogamous pair bonds of humans and other mammalian species (Carter,

2014; MacDonald & MacDonald, 2010). Future research should examine whether the asocial nature of the goody bag paradigm obstructed the social nature of the charitable act, which might be essential to observe positive links between individual differences in the oxytocin receptor gene and the positive mood benefits of helping.⁶

In the current study, we focused on positive mood; however, our findings do not rule out the possibility that individual differences in the oxytocin system predict other emotional responses to helping, such as enhanced feelings of social connection (e.g., Hutcher, Seppala, & Gross, 2008). Given that individual differences in the oxytocin system shape social responsiveness (Li et al., 2015), individual genetic differences might be more predictive of interpersonally relevant positive emotions such as gratitude and appreciation rather than general positive emotions. Indirect evidence for this idea arises from research examining how the oxytocin system shapes the benefits of gratitude. In one paper, across two studies, researchers did not observe a link between individual differences in the oxytocin system, expressing or receiving gratitude, and increased positive mood (Algoe & Way, 2014; Algoe et al., 2017). In contrast to the null results on positive mood, the authors observed a direct association between oxytocin and feelings of appreciation: People who expressed gratitude toward someone that they had a close relationship with felt more cared for, understood, and validated by this person, and these results were moderated by individual differences in the oxytocin system (Algoe et al., 2017). In addition, prior research that examines the causal impact of intranasal oxytocin has often observed no direct effect of intranasal oxytocin administration on positive mood (Buchheim et al., 2009; Guastella, Mitchell, & Dadds, 2008; Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005; Unkelbach, Guastella, & Forgas, 2008). Considered together, these results increase the theoretical precision in predictions about the behavioral and psychological mechanisms related to the oxytocin system (see Algoe et al., 2017 for a similar discussion). We encourage researchers to measure both positive mood and interpersonal emotions to best understand the role of oxytocin in shaping the mood benefits of helping others.

⁶ Another potential limitation of using the goody bag paradigm is that participants were randomly assigned to purchase a goody bag filled with edible treats for themselves or for a sick child at a local children's hospital. Although providing the opportunity to purchase desirable items is necessary to allow an unbiased assessment of personal and prosocial spending, participants may have felt worried or guilty about giving sugary treats to a sick child. As such, future researchers may wish to use other desirable items (e.g., stickers) to avoid this concern. Critically, however, this limitation does not undermine evidence for the positive mood benefits of giving. If anything, this concern suggests that the current study was a conservative test of our hypothesis: If participants had purchased a different desirable item, they might have experienced less discomfort providing the treats and experienced greater positive mood benefits from giving.

Table 8
Bayesian Analysis of Variance Model Comparisons for the Effects of rs2268498

Models	P(M)	P(M data)	BF _M	BF ₁₀	error%
Condition	.333	.723	5.227	1.000	
Condition + rs2268498	.333	.207	.522	.286	1.032
Condition + rs2268498 + Condition × rs2268498	.333	.070	.150	.096	1.861

Relatedly, preliminary evidence suggests that the extent to which oxytocin moderates the mood benefits of helping others could depend on the response of the recipient (see the [online supplemental material](#); Algoe et al., 2017). In one study, circulating levels of oxytocin predicted how connected people felt after expressing gratitude, but only when the recipient positively acknowledged their gratitude expression. These data are consistent with research showing that individuals reap the greatest positive mood benefits from spending money on others when they can observe the direct impact that their actions have for another person (Aknin, Dunn, Whillans, Grant, & Norton, 2013). Future work should examine whether the recipients' response predicts whether the oxytocin system influences the positive mood benefits of helping other people.

More broadly, future research should focus on other forms of generosity. In this study, we focused only on one form of generosity—spending money on others. Although past research has shown that both spending money and time helping others are profitable pathways to greater SWB (Dunn et al., 2014; Mogilner, Chance, & Norton, 2012; Mogilner, Whillans, & Norton, 2018), future research could examine whether individual genetic differences are better predictors of the emotional benefits of longer-term prosocial investments (e.g., volunteering for a local cause) as compared to short-term helping behaviors (e.g., making a one-time financial donation). More formally examining the types of helping situations moderated by individual genetic differences would further the theoretical understanding in this area about the associations between neurobiology, prosocial behavior, and physical and psychological health.

We should note that the results that we observed between prosocial spending and positive mood were small. The effect sizes that we documented were slightly smaller yet consistent with past published research in this area (see Hanniball, Aknin, Douglas, & Viljoen, 2018 for an overview). The effect sizes that we observed in this tightly controlled experiment are consistent with the diminutive effects that are often observed between small actions and the multiply determined construct of well-being (see: Fredrickson, 2001; Lyubomirsky et al., 2005). Because small changes in mood can accumulate into meaningful changes in SWB over time (Fredrickson, 2001; Whillans, Dunn, Smeets, Bekkers, & Norton, 2017), we believe that these results constitute a conceptually and practically relevant effect. For example, a 0.10 change on a 1 to 5 scale constitutes an effect that is about half the size of getting divorced, which is a life change that has been shown in the literature to have one of the strongest effects on daily mood and SWB (Lucas, Clark, Georgellis, & Diener, 2003; Lucas, 2007).

Previous research suggests that we might have observed larger benefits of prosocial spending if we had recruited at-risk populations. For example, in one study, researchers tracked a group of nearly 100 youth over 10 days (Schacter & Margolin, 2018). All

participants experienced greater positive mood on days where they engaged in prosocial behavior (controlling for the help they received). The positive mood benefits of helping others were strongest for individuals who experienced the greatest depressive symptoms. Research has also found evidence that carriers of alleles that are typically associated with lower levels of social functioning, experience the greatest benefits from volunteering and donating (Poulin & Holman, 2013). Thus, future research should also attempt to replicate this research among more stressed or vulnerable populations who might stand to benefit most from helping other people (see Aknin et al., in press, for a review).

In sum, we have used Bayesian analyses to provide evidence that three commonly studied individual differences in the oxytocin receptor gene do not predict the positive mood benefits of prosocial spending. By doing so, it is our hope that the current research facilitates future research to examine the specific conditions by which individual differences in the oxytocin receptor gene influence the social and emotional consequences of prosocial behavior.

References

- Abdel-Khalek, A. M. (2006). Measuring happiness with a single-item scale. *Social Behavior and Personality: An International Journal*, *34*, 139–150. <http://dx.doi.org/10.2224/sbp.2006.34.2.139>
- Aknin, L. B., Barrington-Leigh, C. P., Dunn, E. W., Helliwell, J., Burns, J., Biswas-Diener, R., . . . Norton, M. I. (2013). Prosocial spending and well-being: Cross-cultural evidence for a psychological universal. *Journal of Personality and Social Psychology*, *104*, 635–652. <http://dx.doi.org/10.1037/a0031578>
- Aknin, L. B., Broesch, T., Hamlin, J. K., & Van de Vondervoort, J. W. (2015). Prosocial behavior leads to happiness in a small-scale rural society. *Journal of Experimental Psychology: General*, *144*, 788–795. <http://dx.doi.org/10.1037/xge0000082>
- Aknin, L. B., Dunn, E. W., Whillans, A. V., Grant, A. M., & Norton, M. I. (2013). Making a difference matters: Impact unlocks the emotional benefits of prosocial spending. *Journal of Economic Behavior & Organization*, *88*, 90–95. <http://dx.doi.org/10.1016/j.jebo.2013.01.008>
- Aknin, L. B., Hamlin, J. K., & Dunn, E. W. (2012). Giving leads to happiness in young children. *PLoS ONE*, *7*(6), e39211. <http://dx.doi.org/10.1371/journal.pone.0039211>
- Aknin, L. B., Van de Vondervoort, J. W., & Hamlin, J. K. (2018). Positive feelings reward and promote prosocial behavior. *Current Opinion in Psychology*, *20*, 55–59. <http://dx.doi.org/10.1016/j.copsyc.2017.08.017>
- Aknin, L. B., Whillans, A. V., Dunn, E. W., & Norton, M. I. (in press). Happiness and prosocial behavior: An evaluation of the evidence. *World Happiness Report*.
- Algoe, S. B., Kurtz, L. E., & Grewen, K. (2017). Oxytocin and social bonds: The role of oxytocin in perceptions of romantic partners' bonding behavior. *Psychological Science*, *28*, 1763–1772. <http://dx.doi.org/10.1177/09567976177116922>
- Algoe, S. B., & Way, B. M. (2014). Evidence for a role of the oxytocin system, indexed by genetic variation in CD38, in the social bonding

- effects of expressed gratitude. *Social Cognitive and Affective Neuroscience*, 9, 1855–1861. <http://dx.doi.org/10.1093/scan/nst182>
- Anacker, A., & Beery, A. (2013). Life in groups: The roles of oxytocin in mammalian sociality. *Frontiers in Behavioral Neuroscience*, 7, 185. <http://dx.doi.org/10.3389/fnbeh.2013.00185>
- Apter-Levy, Y., Feldman, M., Vakart, A., Ebstein, R. P., & Feldman, R. (2013). Impact of maternal depression across the first 6 years of life on the child's mental health, social engagement, and empathy: The moderating role of oxytocin. *The American Journal of Psychiatry*, 170, 1161–1168. <http://dx.doi.org/10.1176/appi.ajp.2013.12121597>
- Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2008). Oxytocin receptor (OXTR) and serotonin transporter (5-HTT) genes associated with observed parenting. *Social Cognitive and Affective Neuroscience*, 3, 128–134. <http://dx.doi.org/10.1093/scan/nsn004>
- Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2014). A sociability gene? Meta-analysis of oxytocin receptor genotype effects in humans. *Psychiatric Genetics*, 24, 45–51. <http://dx.doi.org/10.1097/YPG.0b013e3283643684>
- Bartz, J. A., Zaki, J., Bolger, N., & Ochsner, K. N. (2011). Social effects of oxytocin in humans: Context and person matter. *Trends in Cognitive Sciences*, 15, 301–309. <http://dx.doi.org/10.1016/j.tics.2011.05.002>
- Bekkers, R., Konrath, S. H., & Smith, D. H. (2016). Physiological correlates of volunteering. In D. H. Smith, R. A. Stebbins, & J. Grotz (Eds.), *The Palgrave handbook of volunteering, civic participation, and non-profit associations* (pp. 541–579). London, UK: Palgrave Macmillan. http://dx.doi.org/10.1007/978-1-137-26317-9_26
- Borgonovi, F. (2008). Doing well by doing good. The relationship between formal volunteering and self-reported health and happiness. *Social Science & Medicine*, 66, 2321–2334. <http://dx.doi.org/10.1016/j.socscimed.2008.01.011>
- Brown, S. L., Nesse, R. M., Vinokur, A. D., & Smith, D. M. (2003). Providing social support may be more beneficial than receiving it: Results from a prospective study of mortality. *Psychological Science*, 14, 320–327. <http://dx.doi.org/10.1111/1467-9280.14461>
- Buchheim, A., Heinrichs, M., George, C., Pokorny, D., Koops, E., Henningsen, P., . . . Gundel, H. (2009). Oxytocin enhances the experience of attachment security. *Psychoneuroendocrinology*, 34, 1417–1422. <http://dx.doi.org/10.1016/j.psyneuen.2009.04.002>
- Butovskaya, P. R., Lazebny, O. E., Sukhodolskaya, E. M., Vasiliev, V. A., Dronova, D. A., Fedenok, J. N., . . . Butovskaya, M. L. (2016). Polymorphisms of two loci at the oxytocin receptor gene in populations of Africa, Asia and South Europe. *BMC Genetics*, 17, 17. <http://dx.doi.org/10.1186/s12863-015-0323-8>
- Cardon, L. R., & Palmer, L. J. (2003). Population stratification and spurious allelic association. *Lancet*, 361, 598–604. [http://dx.doi.org/10.1016/S0140-6736\(03\)12520-2](http://dx.doi.org/10.1016/S0140-6736(03)12520-2)
- Carter, C. S. (2014). Oxytocin pathways and the evolution of human behavior. *Annual Review of Psychology*, 65, 17–39. <http://dx.doi.org/10.1146/annurev-psych-010213-115110>
- Chen, F. S., Barth, M. E., Johnson, S. L., Gotlib, I. H., & Johnson, S. C. (2011). Oxytocin receptor (OXTR) polymorphisms and attachment in human infants. *Frontiers in Developmental Psychology*, 2, 200. <http://dx.doi.org/10.3389/fpsyg.2011.00200>
- Chen, F. S., Heinrichs, M., & Johnson, S. C. (2017). Oxytocin and the emergence of individual differences in the social regulation of stress. *Social Personality and Psychology Compass*, 11, e12332. <http://dx.doi.org/10.1111/spc3.12332>
- Chen, F. S., Kumsta, R., von Dawans, B., Monakhov, M., Ebstein, R. P., & Heinrichs, M. (2011). Common oxytocin receptor gene (OXTR) polymorphism and social support interact to reduce stress in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 19937–19942. <http://dx.doi.org/10.1073/pnas.11113079108>
- Creaven, A. M., Healy, A., & Howard, S. (2018). Social connectedness and depression: Is there added value in volunteering? *Journal of Social and Personal Relationships*, 35, 1400–1417. <http://dx.doi.org/10.1177/0265407517716786>
- Decety, J., Bartal, I. B. A., Uzevovsky, F., & Knafo-Noam, A. (2016). Empathy as a driver of prosocial behaviour: Highly conserved neurobehavioural mechanisms across species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 20150077.
- Deci, E. L., La Guardia, J. G., Moller, A. C., Scheiner, M. J., & Ryan, R. M. (2006). On the benefits of giving as well as receiving autonomy support: Mutuality in close friendships. *Personality and Social Psychology Bulletin*, 32, 313–327. <http://dx.doi.org/10.1177/0146167205282148>
- Diener, E. D., Emmons, R. A., Larsen, R. J., & Griffin, S. (1985). The satisfaction with life scale. *Journal of Personality Assessment*, 49, 71–75. http://dx.doi.org/10.1207/s15327752jpa4901_13
- Diener, E., & Lucas, R. (1999). Personality and subjective well-being. In D. Kahneman, E. Diener, & N. Schwarz (Eds.), *Well-being: The foundations of hedonic psychology*. New York, NY: Russell-Sage.
- Dunn, E. W., Aknin, L. B., & Norton, M. I. (2008). Spending money on others promotes happiness. *Science*, 319, 1687–1688. <http://dx.doi.org/10.1126/science.1150952>
- Dunn, E. W., Aknin, L. B., & Norton, M. I. (2014). Prosocial spending and happiness: Using money to benefit others pays off. *Current Directions in Psychological Science*, 23, 41–47. <http://dx.doi.org/10.1177/0963721413512503>
- Ebstein, R. P., Knafo, A., Mankuta, D., Chew, S. H., & San Lai, P. (2012). The contributions of oxytocin and vasopressin pathway genes to human behavior. *Hormones and Behavior*, 61, 359–379. <http://dx.doi.org/10.1016/j.yhbeh.2011.12.014>
- Feldman, R., Zagoory-Sharon, O., Weisman, O., Schneiderman, I., Gordon, I., Maoz, R., . . . Ebstein, R. P. (2012). Sensitive parenting is associated with plasma oxytocin and polymorphisms in the OXTR and CD38 genes. *Biological Psychiatry*, 72, 175–181. <http://dx.doi.org/10.1016/j.biopsych.2011.12.025>
- Fredrickson, B. L. (2001). The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions. *American Psychologist*, 56, 218–226. <http://dx.doi.org/10.1037/0003-066X.56.3.218>
- Gong, P., Fan, H., Liu, J., Yang, X., Zhang, K., & Zhou, X. (2017). Revisiting the impact of OXTR rs53576 on empathy: A population-based study and a meta-analysis. *Psychoneuroendocrinology*, 80, 131–136. <http://dx.doi.org/10.1016/j.psyneuen.2017.03.005>
- Guastella, A. J., Mitchell, P. B., & Dadds, M. R. (2008). Oxytocin increases gaze to the eye region of human faces. *Biological Psychiatry*, 63, 3–5. <http://dx.doi.org/10.1016/j.biopsych.2007.06.026>
- Hanniball, K. B., Aknin, L. B., Douglas, K. S., & Viljoen, J. L. (2018). Does helping promote well-being in at-risk youth and ex-offender samples? *Journal of Experimental Social Psychology*. Advance online publication. <http://dx.doi.org/10.1016/j.jesp.2018.11.001>
- Hill, G., & Howell, R. T. (2014). Moderators and mediators of pro-social spending and well-being: The influence of values and psychological need satisfaction. *Personality and Individual Differences*, 69, 69–74. <http://dx.doi.org/10.1016/j.paid.2014.05.013>
- Hong, S. I., & Morrow-Howell, N. (2010). Health outcomes of Experience Corps®: A high-commitment volunteer program. *Social Science & Medicine*, 71, 414–420. <http://dx.doi.org/10.1016/j.socscimed.2010.04.009>
- Hovey, D., Henningson, S., Cortes, D. S., Bänziger, T., Zettergren, A., Melke, J., . . . Westberg, L. (2018). Emotion recognition associated with polymorphism in oxytocinergic pathway gene ARNT2. *Social Cognitive and Affective Neuroscience*, 13, 173–181. <http://dx.doi.org/10.1093/scan/nsx141>

- Hutcherson, C. A., Seppala, E. M., & Gross, J. J. (2008). Loving-kindness meditation increases social connectedness. *Emotion, 8*, 720–724. <http://dx.doi.org/10.1037/a0013237>
- Inoue, H., Yamasue, H., Tochigi, M., Abe, O., Liu, X., Kawamura, Y., . . . Kasai, K. (2010). Association between the oxytocin receptor gene and amygdalar volume in healthy adults. *Biological Psychiatry, 68*, 1066–1072. <http://dx.doi.org/10.1016/j.biopsych.2010.07.019>
- Isen, A. M. (1970). Success, failure, attention, and reaction to others: The warm glow of success. *Journal of Personality and Social Psychology, 15*, 294–301. <http://dx.doi.org/10.1037/h0029610>
- Isen, A. M., & Levin, P. F. (1972). Effect of feeling good on helping: Cookies and kindness. *Journal of Personality and Social Psychology, 21*, 384–388. <http://dx.doi.org/10.1037/h0032317>
- Isgett, S. F., Algoe, S. B., Boulton, A. J., Way, B. M., & Fredrickson, B. L. (2016). Common variant in OXTR predicts growth in positive emotions from loving-kindness training. *Psychoneuroendocrinology, 73*, 244–251. <http://dx.doi.org/10.1016/j.psyneuen.2016.08.010>
- Isgett, S. F., Kok, B. E., Baczkowski, B. M., Algoe, S. B., Grewen, K. M., & Fredrickson, B. L. (2017). Influences of oxytocin and respiratory sinus arrhythmia on emotions and social behavior in daily life. *Emotion, 17*, 1156–1165. <http://dx.doi.org/10.1037/emo0000301>
- Israel, S., Weisel, O., Ebstein, R. P., & Bornstein, G. (2012). Oxytocin, but not vasopressin, increases both parochial and universal altruism. *Psychoneuroendocrinology, 37*, 1341–1344. <http://dx.doi.org/10.1016/j.psyneuen.2012.02.001>
- Jenkinson, C. E., Dickens, A. P., Jones, K., Thompson-Coon, J., Taylor, R. S., Rogers, M., . . . Richards, S. H. (2013). Is volunteering a public health intervention? A systematic review and meta-analysis of the health and survival of volunteers. *BMC Public Health, 13*, 773. <http://dx.doi.org/10.1186/1471-2458-13-773>
- Kashdan, T. B., Biswas-Diener, R., & King, L. A. (2008). Reconsidering happiness: The costs of distinguishing between hedonics and eudaimonia. *The Journal of Positive Psychology, 3*, 219–233. <http://dx.doi.org/10.1080/17439760802303044>
- Kim, H. S., Sherman, D. K., Sasaki, J. Y., Xu, J., Chu, T. Q., Ryu, C., . . . Taylor, S. E. (2010). Culture, distress, and oxytocin receptor polymorphism (OXTR) interact to influence emotional support seeking. *Proceedings of the National Academy of Sciences of the United States of America, 107*, 15717–15721. <http://dx.doi.org/10.1073/pnas.1010830107>
- Klein, N. (2017). Prosocial behavior increases perceptions of meaning in life. *The Journal of Positive Psychology, 12*, 354–361. <http://dx.doi.org/10.1080/17439760.2016.1209541>
- Kogan, A., Saslow, L. R., Impett, E. A., Oveis, C., Keltner, D., & Saturn, S. R. (2011). Thin-slicing study of the oxytocin receptor (OXTR) gene and the evaluation and expression of the prosocial disposition. *Proceedings of the National Academy of Sciences of the United States of America, 108*, 19189–19192. <http://dx.doi.org/10.1073/pnas.1112658108>
- Konrath, S. (2014). The power of philanthropy and volunteering. In C. L. Cooper (Ed.), *Wellbeing: A Complete reference guide, interventions and policies to enhance wellbeing*. West Sussex, UK: Wiley Ltd. <http://dx.doi.org/10.1002/9781118539415.wbwell046>
- Konrath, S., & Brown, S. (2013). The effects of giving on givers. In N. A. Roberts & M. Newman (Eds.), *Health and social relationships: The good, the bad, and the complicated* (pp. 39–64). Washington, DC: American Psychological Association.
- Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U., & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature, 435*, 673–676. <http://dx.doi.org/10.1038/nature03701>
- Krueger, F., Parasuraman, R., Iyengar, V., Thornburg, M., Weel, J., Lin, M., . . . Lipsky, R. H. (2012). Oxytocin receptor genetic variation promotes human trust behavior. *Frontiers in Human Neuroscience, 6*, 4. <http://dx.doi.org/10.3389/fnhum.2012.00004>
- Kumsta, R., & Heinrichs, M. (2013). Social neuropeptides, stress and approach behavior: Neurogenetics of the human oxytocin system. *Current Opinion in Neurobiology, 23*, 11–16. <http://dx.doi.org/10.1016/j.conb.2012.09.004>
- Lane, A., Luminet, O., Nave, G., & Mikolajczak, M. (2016). Is there a publication bias in behavioural intranasal oxytocin research on humans? Opening the file drawer of one laboratory. *Journal of Neuroendocrinology, 28*. <http://dx.doi.org/10.1111/jne.12384>
- Leng, G., & Ludwig, M. (2016). Intranasal oxytocin: Myths and delusions. *Biological Psychiatry, 79*, 243–250. <http://dx.doi.org/10.1016/j.biopsych.2015.05.003>
- Leppanen, J., Ng, K. W., Tchanturia, K., & Treasure, J. (2017). Meta-analysis of the effects of intranasal oxytocin on interpretation and expression of emotions. *Neuroscience and Biobehavioral Reviews, 78*, 125–144. <http://dx.doi.org/10.1016/j.neubiorev.2017.04.010>
- Li, J., Zhao, Y., Li, R., Broster, L. S., Zhou, C., & Yang, S. (2015). Association of oxytocin receptor gene (OXTR) rs53576 polymorphism with sociality: A meta-analysis. *PLoS ONE, 10*(6), e0131820. <http://dx.doi.org/10.1371/journal.pone.0131820>
- Linnér, R. K., Biroli, P., Kong, E., Meddens, S. F. W., Wedow, R., Fontana, M. A., . . . Beauchamp, J. P. (2018). Genome-wide study identifies 611 loci associated with risk tolerance and risky behaviors. *bioRxiv*. Advance online publication. <http://dx.doi.org/10.1101/261081>
- Lishner, D. A., Batson, C. D., & Huss, E. (2011). Tenderness and sympathy: Distinct empathic emotions elicited by different forms of need. *Personality and Social Psychology Bulletin, 37*, 614–625. <http://dx.doi.org/10.1177/0146167211403157>
- LoParo, D., & Waldman, I. D. (2015). The oxytocin receptor gene (OXTR) is associated with autism spectrum disorder: A meta-analysis. *Molecular Psychiatry, 20*, 640–646. <http://dx.doi.org/10.1038/mp.2014.77>
- Lucas, R. E. (2007). Adaptation and the set-point model of subjective well-being: Does happiness change after major life events? *Current Directions in Psychological Science, 16*, 75–79. <http://dx.doi.org/10.1111/j.1467-8721.2007.00479.x>
- Lucas, R. E., Clark, A. E., Georgellis, Y., & Diener, E. (2003). Reexamining adaptation and the set point model of happiness: Reactions to changes in marital status. *Journal of Personality and Social Psychology, 84*, 527–539. <http://dx.doi.org/10.1037/0022-3514.84.3.527>
- Lukas, M., Toth, I., Reber, S. O., Slattery, D. A., Veenema, A. H., & Neumann, I. D. (2011). The neuropeptide oxytocin facilitates pro-social behavior and prevents social avoidance in rats and mice. *Neuropsychopharmacology, 36*, 2159–2168. <http://dx.doi.org/10.1038/npp.2011.95>
- Lyubomirsky, S., & Lepper, H. S. (1999). A measure of subjective happiness: Preliminary reliability and construct validation. *Social Indicators Research, 46*, 137–155. <http://dx.doi.org/10.1023/A:1006824100041>
- Lyubomirsky, S., Sheldon, K. M., & Schkade, D. (2005). Pursuing happiness: The architecture of sustainable change. *Review of General Psychology, 9*, 111–131. <http://dx.doi.org/10.1037/1089-2680.9.2.111>
- MacDonald, K., & MacDonald, T. M. (2010). The peptide that binds: A systematic review of oxytocin and its prosocial effects in humans. *Harvard Review of Psychiatry, 18*, 1–21. <http://dx.doi.org/10.3109/10673220903523615>
- McCullough, M. E., Churchland, P. S., & Mendez, A. J. (2013). Problems with measuring peripheral oxytocin: Can the data on oxytocin and human behavior be trusted? *Neuroscience and Biobehavioral Reviews, 37*, 1485–1492. <http://dx.doi.org/10.1016/j.neubiorev.2013.04.018>
- McGuire, A. M. (1994). Helping behaviors in the natural environment: Dimensions and correlates of helping. *Personality and Social Psychology Bulletin, 20*, 45–56. <http://dx.doi.org/10.1177/0146167294201004>
- Melchers, M., Montag, C., Felten, A., & Reuter, M. (2015). The oxytocin receptor gene and social perception. *Social Neuroscience, 10*, 345–353. <http://dx.doi.org/10.1080/17470919.2015.1008646>
- Melchers, M., Montag, C., Markett, S., Niaz, N., Groß-Böling, J., Zimmermann, J., & Reuter, M. (2017). The OXTR gene, implicit learning

- and social processing: Does empathy evolve from perceptual skills for details? *Behavioural Brain Research*, 329, 35–40. <http://dx.doi.org/10.1016/j.bbr.2017.04.036>
- Melchers, M., Montag, C., Markett, S., & Reuter, M. (2013). Relationship between oxytocin receptor genotype and recognition of facial emotion. *Behavioral Neuroscience*, 127, 780–787. <http://dx.doi.org/10.1037/a0033748>
- Menon, R., Grund, T., Zoicas, I., Althammer, F., Fiedler, D., Biermeier, V., . . . Neumann, I. D. (2018). Oxytocin signaling in the lateral septum prevents social fear during lactation. *Current Biology*, 28, 1066–1078. <http://dx.doi.org/10.1016/j.cub.2018.02.044>
- Mogilner, C., Chance, Z., & Norton, M. I. (2012). Giving time gives you time. *Psychological Science*, 23, 1233–1238. <http://dx.doi.org/10.1177/0956797612442551>
- Mogilner, C., Whillans, A. V., & Norton, M. I. (2018). Time, money, and subjective well-being. In E. Diener, S. Oishi, & L. Tay (Eds.), *Handbook of well-being: Noba Scholar handbook series: Subjective well-being* (pp. 1–26) Salt Lake City, UT: DEF Publishers.
- Montag, C., Fiebach, C. J., Kirsch, P., & Reuter, M. (2011). Interaction of 5-HTTLPR and a variation on the oxytocin receptor gene influences negative emotionality. *Biological Psychiatry*, 69, 601–603. <http://dx.doi.org/10.1016/j.biopsych.2010.10.026>
- Morey, R. D., & Rouder, J. N. (2015). BayesFactor (Version 0.9.11–3) [Computer software]. Retrieved from <https://zenodo.org/record/14950#.XlJKtRNKgb0>
- Musick, M. A., & Wilson, J. (2003). Volunteering and depression: The role of psychological and social resources in different age groups. *Social Science & Medicine*, 56, 259–269. [http://dx.doi.org/10.1016/S0277-9536\(02\)00025-4](http://dx.doi.org/10.1016/S0277-9536(02)00025-4)
- Nave, G., Camerer, C., & McCullough, M. (2015). Does oxytocin increase trust in humans? A critical review of research. *Perspectives on Psychological Science*, 10, 772–789. <http://dx.doi.org/10.1177/1745691615600138>
- Nelson, S. K., Layous, K., Cole, S. W., & Lyubomirsky, S. (2016). Do unto others or treat yourself? The effects of prosocial and self-focused behavior on psychological flourishing. *Emotion*, 16, 850–861. <http://dx.doi.org/10.1037/emo0000178>
- Park, S. Q., Kahnt, T., Dogan, A., Strang, S., Fehr, E., & Tobler, P. N. (2017). A neural link between generosity and happiness. *Nature Communications*, 8, 15964. <http://dx.doi.org/10.1038/ncomms15964>
- Pearce, P. L., & Amato, P. R. (1980). A taxonomy of helping: A multidimensional scaling analysis. *Social Psychology Quarterly*, 43, 363–371. <http://dx.doi.org/10.2307/3033956>
- Pedersen, C. A., Ascher, J. A., Monroe, Y. L., & Prange, A. J. (1982). Oxytocin induces maternal behavior in virgin female rats. *Science*, 216, 648–650. <http://dx.doi.org/10.1126/science.7071605>
- Penner, L. A., Dovidio, J. F., Piliavin, J. A., & Schroeder, D. A. (2005). Prosocial behavior: Multilevel perspectives. *Annual Review of Psychology*, 56, 365–392. <http://dx.doi.org/10.1146/annurev.psych.56.091103.070141>
- Piliavin, J. A., & Siegl, E. (2007). Health benefits of volunteering in the Wisconsin longitudinal study. *Journal of Health and Social Behavior*, 48, 450–464. <http://dx.doi.org/10.1177/002214650704800408>
- Poulin, M. J., Brown, S. L., Dillard, A. J., & Smith, D. M. (2013). Giving to others and the association between stress and mortality. *American Journal of Public Health*, 103, 1649–1655. <http://dx.doi.org/10.2105/AJPH.2012.300876>
- Poulin, M. J., & Holman, E. A. (2013). Helping hands, healthy body? Oxytocin receptor gene and prosocial behavior interact to buffer the association between stress and physical health. *Hormones and Behavior*, 63, 510–517. <http://dx.doi.org/10.1016/j.yhbeh.2013.01.004>
- Poulin, M. J., Holman, E. A., & Buffone, A. (2012). The neurogenetics of nice: Receptor genes for oxytocin and vasopressin interact with threat to predict prosocial behavior. *Psychological Science*, 23, 446–452. <http://dx.doi.org/10.1177/0956797611428471>
- Raposa, E. B., Laws, H. B., & Ansell, E. B. (2016). Prosocial behavior mitigates the negative effects of stress in everyday life. *Clinical Psychological Science*, 4, 691–698. <http://dx.doi.org/10.1177/2167702615611073>
- Reuter, M., Montag, C., Altmann, S., Bendlow, F., Elger, C., Kirsch, P., . . . Felten, A. (2017). Functional characterization of an oxytocin receptor gene variant (rs2268498) previously associated with social cognition by expression analysis in vitro and in human brain biopsy. *Social Neuroscience*, 12, 604–611. <http://dx.doi.org/10.1080/17470919.2016.1214174>
- Rietveld, C. A., Medland, S. E., Derringer, J., Yang, J., Esko, T., Martin, N. W., . . . Albrecht, E. (2013). GWAS of 126,559 individuals identifies genetic variants associated with educational attainment. *Science*, 340, 1235488. <http://dx.doi.org/10.1126/science.1235488>
- Rodrigues, S. M., Saslow, L. R., Garcia, N., John, O. P., & Keltner, D. (2009). Oxytocin receptor genetic variation relates to empathy and stress reactivity in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 21437–21441. <http://dx.doi.org/10.1073/pnas.0909579106>
- Rouder, J. N., Morey, R. D., Speckman, P. L., & Province, J. M. (2012). Default Bayes factors for ANOVA designs. *Journal of Mathematical Psychology*, 56, 356–374. <http://dx.doi.org/10.1016/j.jmp.2012.08.001>
- Saphire-Bernstein, S., Way, B. M., Kim, H. S., Sherman, D. K., & Taylor, S. E. (2011). Oxytocin receptor gene (OXTR) is related to psychological resources. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 15118–15122. <http://dx.doi.org/10.1073/pnas.1113137108>
- Schacter, H. L., & Margolin, G. (2018). When it feels good to give: Depressive symptoms, daily prosocial behavior, and adolescent mood. *Emotion*. Advance online publication. <http://dx.doi.org/10.1037/emo0000494>
- Schreier, H. M., Schonert-Reichl, K. A., & Chen, E. (2013). Effect of volunteering on risk factors for cardiovascular disease in adolescents: A randomized controlled trial. *Journal of the American Medical Association Pediatrics*, 167, 327–332. <http://dx.doi.org/10.1001/jamapediatrics.2013.1100>
- Schwartz, C. E., & Sendor, R. M. (1999). Helping others helps oneself: Response shift effects in peer support. *Social Science & Medicine*, 48, 1563–1575. [http://dx.doi.org/10.1016/S0277-9536\(99\)00049-0](http://dx.doi.org/10.1016/S0277-9536(99)00049-0)
- Shamay-Tsoory, S. G., & Abu-Akel, A. (2016). The social salience hypothesis of oxytocin. *Biological Psychiatry*, 79, 194–202. <http://dx.doi.org/10.1016/j.biopsych.2015.07.020>
- Telzer, E. H., Masten, C. L., Berkman, E. T., Lieberman, M. D., & Fuligni, A. J. (2010). Gaining while giving: An fMRI study of the rewards of family assistance among white and Latino youth. *Social Neuroscience*, 5, 508–518.
- Terris, E. T., Beavin, L. E., Barraza, J. A., Schloss, J., & Zak, P. J. (2018). Endogenous oxytocin release eliminates in-group bias in monetary transfers with perspective-taking. *Frontiers in Behavioral Neuroscience*, 12, 35. <http://dx.doi.org/10.3389/fnbeh.2018.00035>
- Thompson, R. J., Parker, K. J., Hallmayer, J. F., Waugh, C. E., & Gotlib, I. H. (2011). Oxytocin receptor gene polymorphism (rs2254298) interacts with familial risk for psychopathology to predict symptoms of depression and anxiety in adolescent girls. *Psychoneuroendocrinology*, 36, 144–147. <http://dx.doi.org/10.1016/j.psychneuen.2010.07.003>
- Tkach, C. T. (2005). *Unlocking the treasury of human kindness: Enduring improvements in mood, happiness, and self-evaluations*. Riverside: University of California.
- Tost, H., Kolachana, B., Hakimi, S., Lemaire, H., Verchinski, B. A., Mattay, V. S., . . . Meyer-Lindenberg, A. (2010). A common allele in the oxytocin receptor gene (OXTR) impacts prosocial temperament and human hypothalamic-limbic structure and function. *Proceedings of the*

- National Academy of Sciences of the United States of America*, 107, 13936–13941. <http://dx.doi.org/10.1073/pnas.1003296107>
- Unkelbach, C., Guastella, A. J., & Forgas, J. P. (2008). Oxytocin selectively facilitates recognition of positive sex and relationship words. *Psychological Science*, 19, 1092–1094. <http://dx.doi.org/10.1111/j.1467-9280.2008.02206.x>
- Van Tongeren, J. D., Green, J. D., Davis, D. E., Hook, J. N., & Hulse, T. L. (2016). Prosociality enhances meaning in life. *The Journal of Positive Psychology*, 11, 225–236. <http://dx.doi.org/10.1080/17439760.2015.1048814>
- Van Willigen, M. (2000). Differential benefits of volunteering across the life course. *The Journals of Gerontology, Series B: Psychological Sciences and Social Sciences*, 55, S308–S318.
- Walum, H., Waldman, I. D., & Young, L. J. (2016). Statistical and methodological considerations for the interpretation of intranasal oxytocin studies. *Biological Psychiatry*, 79, 251–257. <http://dx.doi.org/10.1016/j.biopsych.2015.06.016>
- Watson, D., Clark, L. A., & Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: The PANAS scales. *Journal of Personality and Social Psychology*, 54, 1063–1070. <http://dx.doi.org/10.1037/0022-3514.54.6.1063>
- Weinstein, N., & Ryan, R. M. (2010). When helping helps: Autonomous motivation for prosocial behavior and its influence on well-being for the helper and recipient. *Journal of Personality and Social Psychology*, 98, 222–244. <http://dx.doi.org/10.1037/a0016984>
- Wheeler, J. A., Gorey, K. M., & Greenblatt, B. (1998). The beneficial effects of volunteering for older volunteers and the people they serve: A meta-analysis. *The International Journal of Aging & Human Development*, 47, 69–79. <http://dx.doi.org/10.2190/VUMP-XCMF-FQYU-V0JH>
- Whillans, A. V., Dunn, E. W., Sandstrom, G. M., Dickerson, S. S., & Madden, K. M. (2016). Is spending money on others good for your heart? *Health Psychology*, 35, 574–583. <http://dx.doi.org/10.1037/hea0000332>
- Whillans, A. V., Dunn, E. W., Smeets, P., Bekkers, R., & Norton, M. I. (2017). Buying time promotes happiness. *Proceedings of the National Academy of Sciences of the United States of America*, 201706541.
- Whillans, A. V., Seider, S. C., Chen, L., Dwyer, R. J., Novick, S., Gramigna, K. J., . . . Dunn, E. W. (2016). Does volunteering improve well-being? *Comprehensive Results in Social Psychology*, 1, 35–50. <http://dx.doi.org/10.1080/23743603.2016.1273647>
- Woods, R., Bedard, M., McQuaid, R. J., Matheson, K., & Anisman, H. (2018). Rejection sensitivity and multiple group memberships: The moderating role of an oxytocin receptor gene polymorphism. *Social Neuroscience*, 13, 268–276. <http://dx.doi.org/10.1080/17470919.2017.1327458>

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